www.nsseme.com/journal.html

Genetic Background and Agronomic Value of Leaf Types in Pea (*Pisum sativum*)

Aleksandar Mikić • Vojislav Mihailović • Branko Ćupina • Valentin Kosev • Tom Warkentin • Kevin McPhee • Mike Ambrose • Julie Hofer • Noel Ellis

© 2011 IFVC

Summary: Pea (*Pisum sativum* L.) has a compound leaf like many other legume species. The 'semi-leafless' pea (*afaf TLTL*), with all leaflets transformed into tendrils, is considered one of the most important achievements in pea breeding, due to a significantly enhanced standing ability and equally efficient dry matter production in comparison to normal-leafed genotypes (*AFAF TLTL*). 'Semi-leafless' cultivars provide high and stable grain yield and are dominant in the modern dry pea production worldwide. There are also 'semi-leafless' cultivars that are autumn-sown and those for forage production. The genotypes with all tendrils transformed into leaflets (*AFAF tltl*), called 'acacia' or 'tendril-less', are extremely prone to lodging and may have importance in breeding for forage production. Little is known about the potential agronomic value of 'acacia-tendril-less' (*afaf tltl*) genotypes.

Key words: acacia leaf type, agronomic value, breeding, compound leaf, genetics, pea, *Pisum sativum*, semi-leafless leaf type

Genetics of Pea Leaf Types

Legumes (*Fabaceae*, syn. *Leguminosae*) comprise annual and perennial herbaceous plants, many of which are economically important grain, oilseed and forage crops, as well as shrubs and tropical or subtropical trees. They provide quality protein for humans and animals and enriching the soil by symbiosis with nitrogen-fixing bacteria (Singh et al. 2007). Among the most significant legumes is pea (*Pisum sativum* L.), a true multi-

Figure 1. The *uni* null mutant in pea with normal stipules and only one leaflet (Pisum Genetics Association 2011)

functional crop that may be used as green forage, forage dry matter, forage meal, silage, haylage, immature grain, mature grain, straw and green manure (Mihailović & Mikić 2010). Pea has also been a subject of genetic investigation since the experiments by Thomas Andrew Knight in the 1790s and Gregor Mendel in the 1860s (Ellis 2007, Ellis 2009).

A. Mikić (✉) • V. Mihailović
Institute of Field and Vegetable Crops, Novi Sad, Serbia
e-mail: aleksandar.mikic@ifvcns.ns.ac.rs

B. Ćupina
University of Novi Sad, Faculty of Agriculture, Novi Sad, Serbia

V. Kosev
Institute of Forage Crops, Pleven, Bulgaria

T. Warkentin
University of Saskatchewan, Crop Development Centre, Saskatoon, Canada

K. McPhee
North Dakota State University, Fargo, USA

M. Ambrose
John Innes Centre, Norwich, UK

J. Hofer • N. Ellis
Aberystwyth University, Institute of Biological, Environmental and Rural Sciences, Aberystwyth, UK

The leaves in most legume species are compound (Lewis et al. 2005). Pea, with its pinnately compound leaf consisting of basal, foliaceous stipules, proximal leaflets and distal tendrils, serves as a model species for understanding compound leaf development (Yaxley et al. 2001, Hofer et al. 2009). It is considered that the role of the class 1 *KNOTTED1*-like (*KNOX1*) genes, regulating leaf complexity across vascular plants, in the case of pea and other members of a large subtribe of the *Fabaceae* is taken over by the gene *UNIFOLIATA* (*UNI*), an ortholog of the floral regulators *FLORICAULA* (*FLO*) and *LEAFY* (*LFY*) from the model species *Antirrhinum majus* and *Arabidopsis thaliana* (Gourlay et al. 2000, Champagne et al. 2007). The *UNI* gene is positively regulated by auxin and gibberellin (Bai & DeMason 2006) and maintains the meristematic potential of the compound leaf, enabling the sequential development of pairs of leaflets and tendrils in acropetal order, as shown by *uni* null mutants (Fig. 1), with only a single leaflet (Hofer et al. 1997).

Tendrils are characteristic of the tribe *Fabeae*, to which pea (*Pisum* L.), vetchling (*Lathyrus* L.), vetch (*Vicia* L.), lentil (*Lens* Mill.) and vavilovia (*Vavilovia* Fed.) belong, and some species of the close tribe *Cicereae*. Since nearly all other Papilionoid legumes are untendrilled, it may be assumed that tendrils arose either once, with at least two independent losses, or, twice independently (Hofer et al. 2009).

The size of the stipules in pea is determined by the gene *STIPULES REDUCED* (*ST*), located on the linkage group (LG) III. The wild type has normally developed stipules (*STST*), while the double recessive (*stst*) genotypes are characterised by significantly reduced stipules (Fig. 2). There is the third allele, *ST>BS*, recessive to *ST* and dominant to *st* and responsible for genotypes with 'butterfly stipules', intermediate in size to normal and reduced stipules (Apisitwanich & Swiecicki 1992).

According to an early model of the pea leaf, the structure is determined sequentially during the repeated growth and sub-division of meristems, and secondly, the developmental fate of each meristematic primordium is determined by its size, that is, small primordia become tendrils, intermediate primordial leaflets and large ones rachides (Young 1983). The development of leaflets and tendrils in pea is determined by two genes, *AFILA* (*AF*) on LG I and *TENDRIL-LESS* (*TL*) on LG V. There are four main phenotypes determined by *AF* and *TL* genes (Fig. 3): (1) wild type (*AFAF TLTL*), with two or three pairs of leaflets and numerous tendrils; (2) 'afila' (*afaf TLTL*), with tendrils only; (3) 'clavicula' (*AFAF tltl*), with leaflets only; (4) 'pleiofila' (*afaf tltl*), with rachids ending with small leaflets.

The *AF* gene was described as a mutation by Kujala in 1953, while the *TL* gene was discovered by Vilmorin and Bateson in 1911. The gene *AF* influences pinna length and branching and regulates the timing and direction of leaf developmental processes in its proximal region (Villani & DeMason 1999). The *TL* gene is responsible for transforming lateral organ primordia from their default leaflet fate to a tendril fate where vascular bundles surround the central pith and abaxial-adaxial polarity is suppressed (Hofer et al. 2009). The wild-type *TL* allele probably arose as a semi-dominant mutation, surviving the constraints of selection by providing a novel phenotype and permitting
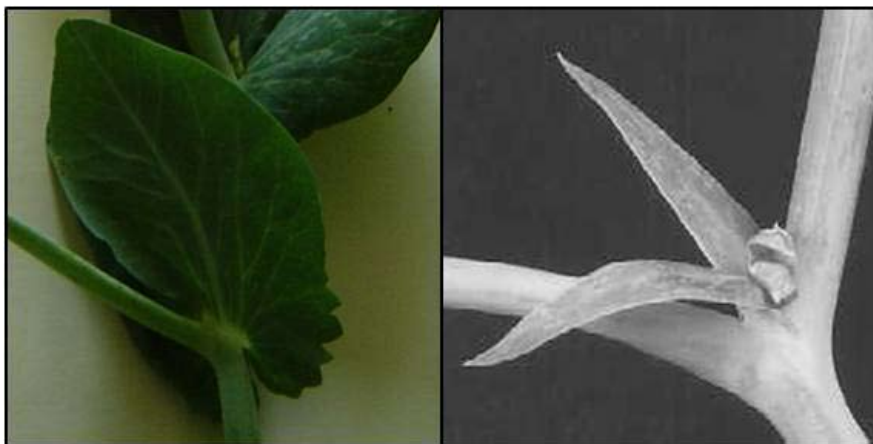

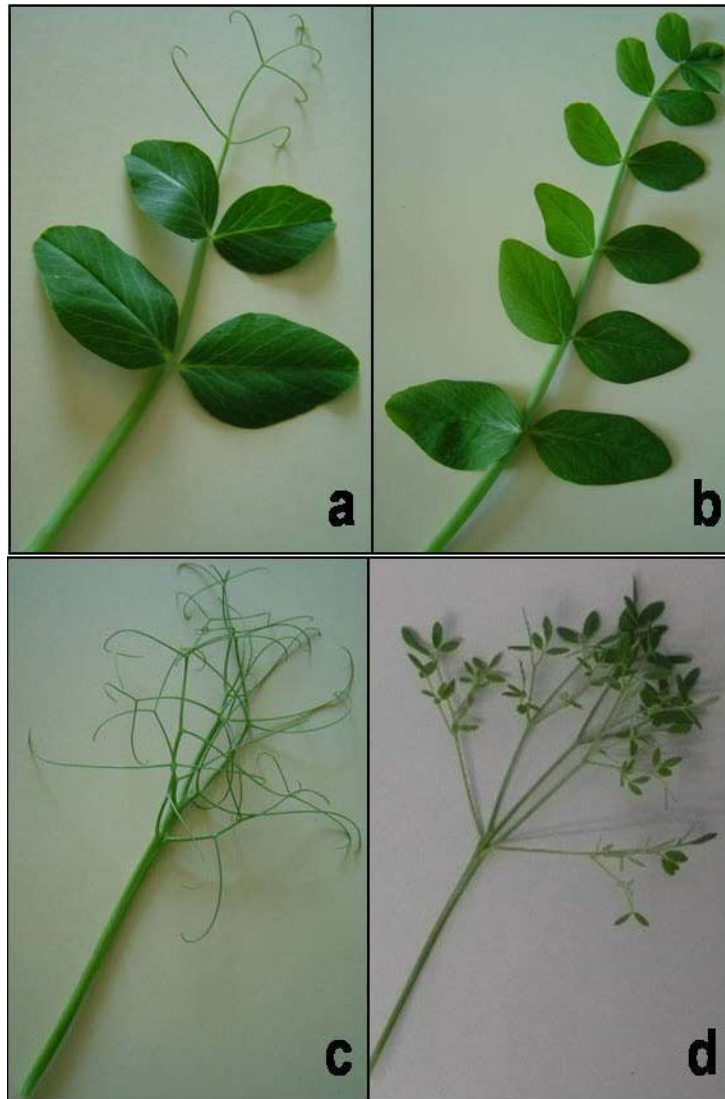Figure 2. Normal (left) and reduced (right) stipules in pea

Figure 3. Four basic types of the pea leaf type, regarding leaflets and tendrils: (A) wild type, (B) *tendril-less*, (C) *afila*, (D) *afila-tendril-less*

adaptation to a new and advantageous climbing growth habit (Hofer et al. 2009). There are reports on novel alleles at both *AF* (Vassileva 1979) and *TL* loci, namely *TL2*, only in the heterozygous state it transforms tendrils into very narrow leaflets (Berdnikov & Gorel 2005), and *TL^{UL}*, with very narrow and elongated, entangling leaflets (Ukrainets 2009).

Agronomy of 'Semi-Leafless' Pea Leaf Type

In the early 1970s, it was suggested that the additional tendrils might improve the standing ability of the pea crop, leading to a wide use of the *AFILA* mutation (Snoad 1974). Its first application was the development of the fully 'leafless' pea (*stst afaf*) ideotype within a pea breeding program at the John Innes Institute and the release of the first UK 'leafless' cultivar Filby (JI 1768) in 1978 (Ambrose 2004). However, although the 'leafless' cultivars were able to produce sufficient photosynthate at normal agronomic densities (Hedley & Ambrose 1979), they failed to do so when grown at low planting densities through a limitation to the total biomass of plants and the crop itself (Hedley & Ambrose 1981). For this reason, the 'leafless' ideotype was largely abandoned and is mostly absent in contemporary pea breeding programmes.

Table 1. Agronomic performance of pea cultivars with conventional and *afila* leaves at Rimski Šančevi during 2000-2002 (Mihailović et al. 2004)

Leaf type	Plant height (cm)	First pod height (cm)	Inter-node number (plant⁻¹)	Pod number (plant⁻¹)	Grain number (plant⁻¹)	1000-grain mass (g)	Plant mass (g)	Grain yield (g plant⁻¹)	Harvest index
AfAf TlTl	65	37	19	8	35	243	13.2	6.9	0.53
afaf TlTl	67	38	19	8	33	258	13.7	7.0	0.53
LSD$_{0.01}$	34.0	13.5	4.7	4.2	14.8	18.1	5.5	3.0	0.07

Table 2. Agronomic performance of pea cultivars with different plant architecture at Rimski Šančevi during 2003-2005 (Mikić et al. 2006a)

Genotype	Plant height (cm)	Number of nodes (plant⁻¹)	Number of pods (plant⁻¹)	Number of grains (plant⁻¹)	Grain yield (g plant⁻¹)	Grain yield (kg ha⁻¹)	Harvest index
Af Det Le	92	23.7	6.0	22.3	4.74	4224	0.39
Af det le	56	19.3	6.0	24.7	5.55	5612	0.48
af det le	56	20.0	5.3	21.0	5.64	5424	0.51
LSD$_{0.01}$	10.2	2.4	5.2	18.4	3.34	994	0.12

Introduction of the *AF* mutation with retained wild type stipules led to the development of 'semi-leafless' pea cultivars that proved superior to 'leafless' in photosynthetic capacity, similar to that of the wild type. This is considered perhaps the greatest achievement in pea breeding (Duparque 1996). The significantly increased standing ability of 'afila' pea cultivars reduced grain yield losses and associated reduction in canopy disease severity (Banniza et al., 2005) increased the interest in cultivating pea as a quality food and feed in many European countries (Mikić et al. 2006b) and in the world. Today, 'semi-leafless' pea cultivars make more than 95% of the total dry pea production in western Canada, about 80% in European Union and more than 30% in Russia. It has to be remarked that the 'afila' leaf type does improve lodging resistance, but on its own does not provide lodging resistance, where stiff stems, in addition to 'afila' leaf type, are also required.

Despite an initial impression that the 'afila' pea stand may be generally less productive, the opposite has been demonstrated in numerous occasions. A detailed physiological study of an 'afila' pea canopy (Kof et al. 2004) revealed that, on one hand, it had a decreased leaf area and a chlorophyll content per plant 1.5-fold lower than the wild type, while, on the other hand, the loss of leaflets was partly recompensed by expansion of the tendrils and stipules, extra accumulation of chlorophyll and increased assimilation area, resulting in enhanced photo-assimilating potential and non-diminished final biomass and grain yield.

The grain yield components of the 'semi-leafless' dry pea cultivars, developed for enhanced and stable dry grain production, do not differ significantly from those in pea cultivars with conventional leaves (Tab. 1), especially if belonging to earlier cultivar generations with indeterminate stem growth (*DET*) and long internodes (*LE*) (Tab. 2). This confirms that 'semi-leafless' pea cultivars, despite a somewhat slower initial growth and development, are at least equally productive as those with conventional leaves, with a considerable advantage regarding standing ability, increased photosynthetic activity of the whole canopy and less favourable conditions for pests and diseases.

An additional benefit of the 'semi-leafless' pea is development of autumn-sown, winter-hardy cultivars, suitable for cultivation in diverse climates (McPhee & Muehlbauer 2007, McPhee et al. 2007), with emphasis upon warmer temperate regions. Such cultivars may contribute to a significant increase of the total

Table 3. Average values of grain yield components and grain yield in various pea types at Rimski Šančevi from 2004 to 2007 (Mihailović et al. 2008)

Type	Plant height (cm)	Number of fertile nodes (plant⁻¹)	Number of pods (plant⁻¹)	Number of grains (plant⁻¹)	Thousand grains mass (g)	Grain yield (kg ha⁻¹)
Winter, normal leaf type	107	7.2	9.8	38.2	117	3348
Winter, afila leaf type	50	3.6	6.6	26.1	206	5236
Spring, normal leaf type	59	3.9	6.3	22.5	236	5215
Spring, afila leaf type	61	3.6	6.0	25.7	233	5252
$LSD_{0.01}$	30	3.6	3.0	12.3	52	1304

Table 4. Average two-year green forage yield (t ha⁻¹), forage dry matter yield (t ha⁻¹) and their Land Equivalent Ratios (LER_{GFY} and LER_{FDMY}) in the mutual intercrops of pea cultivars with different leaf types at Rimski Šančevi during 2008/09 and 2009/10 (Ćupina et al. 2010)

Season	Treatment	Green forage yield of supporting component (*afaf TlTl*)	Green forage yield of supported component (*AfAf TlTl*)	Total green forage yield	LER_{GFY}
Winter	Dove, pure stand	32.4	0.0	32.4	1.00
	Frijaune, pure stand	0.0	30.8	30.8	1.00
	Dove + Frijaune	23.2	11.0	34.2	1.09
Spring	Jezero, pure stand	31.3	0.0	31.3	1.00
	Javor, pure stand	0.0	30.3	30.3	1.00
	Jezero + Javor	16.4	17.5	33.8	1.11
$LSD_{0.05}$			3.7		0.08

Season	Treatment	Forage dry matter yield of supporting component (*afaf TlTl*)	Forage dry matter yield of supported component (*AfAf TlTl*)	Total forage dry matter yield	LER_{FDMY}
Winter	Dove, pure stand	6.8	0.0	6.8	1.00
	Frijaune, pure stand	0.0	7.8	7.8	1.00
	Dove + Frijaune	5.1	3.0	8.1	1.13
Spring	Jezero, pure stand	6.3	0.0	6.3	1.00
	Javor, pure stand	0.0	6.4	6.4	1.00
	Jezero + Javor	2.9	3.6	6.5	1.03
$LSD_{0.05}$			0.8		0.08

Figure 4. The latest Serbian winter dry pea line L-574 (right), registered in November 2010 under the name of the cultivar Mraz, in comparison to the widely used Serbian spring-sown dry pea cultivar Jezero (left), photographed on the same day, May 12, 2009 (Mikić et al. 2011)

Figure 5. Forage 'semi-leafless' pea in the type of cv. CDC Leroy and cv. CDC Tucker

pea cultivation area in many countries (Mikić et al. 2007). Average grain yields in autumn-sown 'semi-leafless' pea cultivars are at the same level as those in the spring-sown 'semi-leafless' and the autumn-sown with conventional leaves (Tab. 3). Most autumn-sown 'semi-leafless' pea cultivars are also characterised by a prominent earliness in comparison to the spring-sown cultivars (Fig. 4). Thus they offer more economic benefit to farmers, especially in central or southern European countries, who often have only one combine harvester available and have to choose between pea and cereals, as a rule giving priority to the latter. Now, with autumn-sown, early 'semi-leafless' pea cultivars, they are provided with a possibility to harvest pea first and then barley or wheat (Mikić et al. 2011).

Pea leaves with large surface areas were not *a priori* large in terms of their dry mass (Niklas et

al. 2008). This opened the possibility to develop 'semi-leafless' cultivars for high and stable forage production (Koivisto 2003, Warkentin et al. 2009), as well as to solve a long-term problem of reliable seed production in forage pea cultivars, since those with conventional leaves often suffer from excessive lodging and high seed losses during the harvest (Karagić et al. 2009). Modern 'semi-leafless' forage pea cultivars (Fig. 5) are characterised by a plant height up to 100 cm, thick and juicy stems, large number of internodes, large stipules comprising up to 76% of the total leaf area (Goldman & Gritton 1992b), tendrils contributing up to 13% of total dry matter (Uzun et al. 2005) and pods grouped in the upper half of a plant (Mihailović et al. 2009). Preliminary research (Ćupina et al. 2010) has demonstrated intercropping pea cultivars with conventional and *afila* leaves may prove economically justified (Tab. 4), offering an alternative to the traditional intecrops of pea with oat (*Avena sativa* L.) or barley (*Hordeum vulgare* L.).

Table 5. Average values of grain yield components and grain yield of pea cultivars with different leaf types at Rimski Šančevi during 2000-2002 (Mihailović & Mikić 2004)

Leaf type	Plant height (cm)	First pod height (cm)	Internode number (plant^{-1})	Pod number (plant^{-1})	Grain number (plant^{-1})	Plant mass (g)	Grain yield (g plant^{-1})	Grain yield (kg ha^{-1})	Harvest index	1000-grain mass (g)
AfAf tltl	69.9	40.8	16.1	8.2	23.3	12.19	5.60	2175	0.46	193
AfAf TlTl	75.2	43.5	18.9	8.7	34.2	15.89	6.97	2217	0.45	244
LSD $_{0,01}$	10.5	6.0	2.4	2.5	12.7	6.96	4.21	1026	0.12	15

Agronomy of 'Acacia' and Other Pea Leaf Types

The agronomic value of the 'acacia' pea cultivars with 'clavicula' leaf type is generally much less studied in comparison to the 'semi-leafless' cultivars or those with conventional leaves. The main reason for this long-term ignorance by agronomists may lie in the fact that such genotypes are extremely prone to lodging due to the lack of tendrils and therefore are immediately recognised as risky for obtaining high and stable grain yields, although their main grain yield components do not have to differ significantly from those in the cultivars with conventional leaves (Tab. 5).

Figure 6. A typical 'acacia' pea plant

The 'acacia' pea genotypes could be interesting in breeding for forage yield (Mihailović & Mikić 2004), with an ideotype with large number of nodes, large stipules, large number of photosynthetically active leaves and pods grouped in the upper half of the plant in order to minimize the losses during harvest (Fig. 6). However, it is still not clear if increasing the total leaf area will lead to a higher forage dry matter production and if an increased leaf proportion in the total forage yield will also result in a higher forage dry matter crude protein content and thus better forage quality. These questions need to be solved by breeding programmes aimed at the development of 'acacia' forage pea cultivars. At this moment, it is likely that such genotypes could be safely cultivated for forage in mixtures with cereals that would serve to support them, since the lodging of 'acacia' pea plants is significant at the stages of full bloom when the crop is usually cut for forage.

Pea with the 'pleiofila' leaf type is a fine example of two-gene interactions where both equally contribute (Marx 1987). In this case, the *af* allele affects marginal meristem function in the leaflet, while the *tl* allele gives rise to adaxial and marginal meristems where none existed before (Meicenheimer et al. 1983). Leaves on the 'pleiofila' plants increase in complexity more rapidly during shoot ontogeny than those on plants with conventional leaves, while leaflets of 'pleiofila' plants have identical histology to wild-type leaflets although with smaller and fewer cells (Villani & DeMason 1997).

Reports on the agronomic performance of the 'pleiofila' pea genotypes are scarce and insufficient for a more detailed comprehensive understanding of their breeding and agronomic value. When grown at a standard highly competitive population density, they do not show any yield improvement compared to those with conventional leaves (Goldman et al. 1992a), however, when grown under minimum competition and in the latest
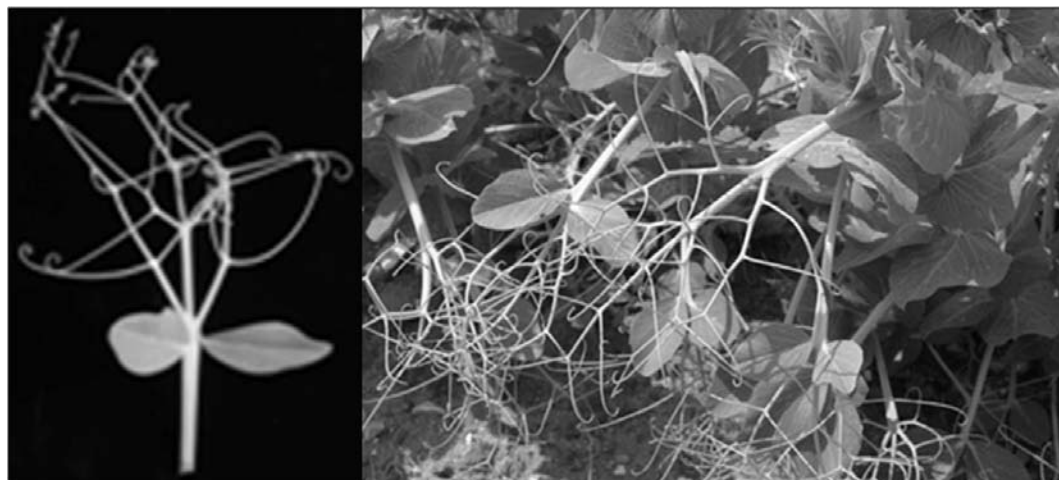
Figure 7. A detail of the leaf (left) and the stand (right) of the 'semi-leafless+' line 11/47 AFILA (JI 3129) developed at the John Innes Centre

maturing background, the 'pleiofila' pea lines may exhibit the largest increases in grain yield in comparison to the genotypes with conventional and 'afila' leaves (Goldman & Gritton 1992, Goldman et al. 1992b).

A few additional leaf mutants in pea could be economically interesting. Among the most interesting examples is a novel mutation at the *AF* locus, weaker than existing alleles, resulting in a pair of leaflets of normal size and morphology or a single leaflet at or just after the ramification of the central rachis (Fig. 7). Such genotypes, referred to as 'semi-leafless+', may be interesting for breeders as the presence of a pair of leaflets at each node may increase the photosynthetic capacity of the plant, enable further increases in biomass at lower densities and increase the leaf area index of a crop early enough in crop development to cut light levels penetrating the crop and thus help suppress emerging weeds (Ambrose 2004). Another mutant, developed at the Institute of Forage Crops in Pleven has four pairs of leaflets on every node and could be interesting for forage production, although the stability of this trait needs to be assessed in diverse environments (Ellis et al. 2009).

Conclusions

Pea has a unique place among the economically important legume species due to its variable leaf morphology. Its genetic background is well studied and provides breeding and other applied research with diverse beneficial possibilities. It may be claimed that the 'semi-leafless' pea cultivars demonstrated the highest level of agronomic utility, playing an essential role in the maintenance and improvement of dry pea production across the world. Other leaf types in pea are less studied but deserve additional evaluation by both geneticists and agronomists, especially in the case of 'acacia' that could have a potential for forage production and 'semi-leafless+' for higher productivity.

References

Ambrose M (2004): A novel allele at the *Afila (Af)* locus and new alleles at the *Tendril-less (Tl)* locus. Pisum Genet. 36: 1-2

Apisitwanich S, Swiecicki W K (1992): A new allele, *st^{hs}*, at the *St* locus. Pisum Genet. 24: 13

Bai F, DeMason D A (2006): Hormone interactions and regulation of *Unifoliata, PsPK2, PsPIN1* and *LE* gene expression in pea *(Pisum sativum)* shoot tips. Plant Cell Physiol. 47: 935-948

Banizza S, Hashemi P, Warkentin T D, Vandenberg A, Davis A R (2005): The relationships among lodging, stem anatomy, degree of lignification, and resistance to mycosphaerella blight in field pea *(Pisum sativum* L.). Can. J. Bot. 83: 954-967

Berdnikov V A, Gorel F L (2005): A mutation, *tl2*, in pea *(Pisum sativum* L.) affects leaf development only in the heterozygous state. Theor. Appl. Genet. 110: 1086-1091

Champagne C E M, Goliber T E, Wojciechowski M F, Mei R W, Townsley B T, Wang K, Paz M M, Geeta R, Sinha N R (2007): Compound leaf development and evolution in the legumes. Plant Cell 19: 3369-3378

Ćupina B, Mikić A, Krstić Đ, Antanasović S, Mihailović V, Erić P, Pejić B (2010): Potential of the intercrops of normal-leafed and semi-leafless pea cultivars for forage production. Pisum Genet. 42: 11-14

Duparque M (1996): Main history steps of the pea improvement. Grain Legum. 12: 18

Ellis T H N (2007): Approaches to the isolation of genes of agronomic importance in pea. Zbornik radova Instituta za ratarstvo i povrtarstvo, Novi Sad 44: 45-47

Ellis T H N (2009): Legume genetics and breeding: the example of pea. Grain Legum. 51: 14-15

Ellis N, Hofer J, Mikić A, Mihailović V, Vasiljević S, Milić D, Đorđević V, Perić V (2009): Leaf types in legumes and their agronomic importance. Abstracts, IV Congress of the Serbian Genetic Society, Tara, Serbia, 165

Goldman I L, Gritton E T (1992a): Evaluation of the afila-tendrilled acacia *(afaf- tactac)* pea foliage type under minimal competition. Crop Sci. 32: 851-855

Goldman I L, Gritton E T (1992b): Seasonal variation in leaf component allocation in normal, afila, and afila-tendrilled acacia pea foliage near-isolines. Am. Soc. Hortic. Sci. 117: 1017-1020

Goldman I L, Gritton E T, Flannery P J (1992): Evaluation of the afila-tendrilled acacia *(afaf- tactac)* pea foliage type under high competition. Crop Sci. 32: 855-861

Gourlay C W, Hofer J M, Ellis T H (2000): Pea compound leaf architecture is regulated by interactions among the genes *UNIFOLIATA, COCHLEATA, AFILA,* and *TENDRIL-LESS.* Plant Cell 12: 1279-1294

Hedley C L, Ambrose M J (1979): The effects of shading on the yield components of six 'leafless' pea genotypes. Ann. Bot. 44: 469-478

Hedley C L, Ambrose M J (1981): Designing 'leafless' plants for improving yields of the dried pea crop. Adv. Agron. 34: 225-277

Hofer J, Turner L, Hellens R, Ambrose M, Matthews P, Michael A, Ellis N (1997): UNIFOLIATA regulates leaf and flower morphogenesis in pea. Curr. Biol. 7: 581-587

Hofer J, Turner L, Moreau C, Ambrose M, Isaac P, Butcher S,Weller J, Dupin A, Dalmais M, Le Signor C, Bendahmane A, Ellis N (2009): *Tendril-less* regulates tendril formation in pea leaves. Plant Cell 21: 420-428

Karagić Đ, Katić S, Mihailović V, Milošević B. (2009): Breeding forage legumes for enhanced seed production. Grain Legum. 51: 30

Kof E M, Oorzhak A S, Vinogradova I A, Kalibernaya Z V, Krendeleva T E, Kukarskikh G P, Kondykov I V, Chuvasheva E S (2004): Leaf morphology, pigment complex, and productivity in wild-type and *afila* pea genotypes. Russ. J. Plant Physiol. 51: 449-454

Koivisto J M, Benjamin L R, Lane G P F, Davies W P (2003): Forage potential of semi-leafless grain peas. Grass Forage Sci. 58: 220-223

Kujala V (1953): Felderbse bei welcher die ganze Blattspreite in Ranken umgewandelt ist. Arch. Soc. Zool. Bot. Fenn. `Vanamo' 8: 44-45

Lewis G P, Schrire B, Mackinder B, Lock M (2005): Legumes of the world. Kew Publishing, Richmond

Marx G A (1987): A suite of mutants that modify pattern formation in pea leaves. Plant Mol Biol Report. 5: 311-335

McPhee K E, Muehlbauer F J (2007): Registration of 'Specter' winter feed pea. J. Plant Regist. 1: 118-119

McPhee K E, Chen C C, Wichman D M, Muehlbauer F J (2007): Registration of 'Windham' winter feed pea. J. Plant Regist. 1: 117-118

Meicenheimer R D, Muehlbauer F J, Hindman J L, Gritton E D (1983): Meristem characteristics of genetically modified pea *(Pisum sativum)* leaf primordia. Can. J. Bot. 61: 3430-3437

Mihailović V, Mikić A (2004): Leaf type and grain yield in forage pea. Genetika 36: 31-38

Mihailović V, Mikić A (2010): Novel directions of breeding annual feed legumes in Serbia. Proceedings, XII International Symposium on Forage Crops of Republic of Serbia, Kruševac, Serbia 1: 81-90

Mihailović V, Erić P, Karagić Đ, Milić D, Mikić A (2004): Grain yield and grain yield components of fodder pea depending on leaf type. Acta Agric. Serb. IX : 17(special issue): 67-71

Mihailović V, Ellis T H N, Duc G, Lejeune-Hénaut I, Étévé G, Angelova S, Mikić A, Ćupina B (2008): Grain yield in winter and spring protein pea cultivars *(Pisum sativum* L.) with normal and afila leaf type. Proceedings, International Conference *Conventional and Molecular Breeding of Field and Vegetable Crops,* Novi Sad, Serbia, 443-446

Mihailović V, Warkentin T, Mikić A, Ćupina B (2009): Challenges for forage pea breeders. Grain Legum. 52: 20-21

Mikić A, Mihailović V, Mikić V, Milić D, Milić S, Terzić S, Balalić I (2006a): Plant architecture and grain yield in feed pea *(Pisum sativum* L.). Proceedings, VIIIth International Symposium *Young People and Multidisciplinary Research,* Timişoara, Romania, 397-402

Mikić A, Mihailović V, Milić D, Vasiljević S, Katić S, Ćupina B (2006b): The role of *af, det* and *le* genes in increasing grain yield of feed pea *(Pisum sativum* L.) in Serbia and Montenegro. Abstracts, 3rd International Conference on Legume Genomics and Genetics, Brisbane, Australia, 109

Mikić A, Mihailović V, Duc G, Ćupina B, Étévé G, Lejeune-Hénaut I, Mikić V (2007): Evaluation of winter protein pea cultivars in the conditions of Serbia. Zbornik radova Instituta za ratarstvo i povrtarstvo, Novi Sad 44: 107-112

Mikić A, Mihailović V, Ćupina B, Đorđević V, Milić D, Duc G, Stoddard F L, Lejeune-Hénaut I, Marget P, Hanocq E (2011): Achievements in breeding winter-sown annual legumes for temperate regions with emphasis on the continental Balkans. Euphytica 180: 57-67

Niklas K J, DeMason D A, Cobb E D (2008): Genetic effects on the biomass partitioning and growth of *Pisum* and *Lycopersicon.* Am. J. Bot. 95: 424-433

Pisum Genetics Association (2011): PGene Pisum Gene List [Online]. [1 p] Available at http://data.jic.bbsrc.ac.uk/cgi-bin/pgene/default.asp (cited 31 March 2011, verified 19 April 2011). John Innes Centre, Norwich

Singh R J, Chung G H, Nelson R L (2007): Landmark research in legumes. Genome 50: 525-537.

Snoad B (1974): A preliminary assessment of 'leafless peas'. Euphytica 23: 257-265

Vassileva M (1979): Induced mutagenesis in *Pisum*. I. Genetic studies on the acacia mutant. Genet. Sel. 12: 396-408

Ukrainets V V (2009): A new pea mutation in the *Tl* Locus. Cytol. Genet. 43: 331-335

Uzun A, Bilgili U, Sincik M, Filya I, Acikgoz E (2005): Yield and quality of forage type pea lines of contrasting leaf types. Eur. J. Agron. 22: 85-94

Villani P J, DeMason D A (1997): Roles of the *af* and *tl* genes in pea leaf morphogenesis: characterization of the double mutant (*afaftltl*). Am. J. Bot. 84: 1323-1336

Villani P J, DeMason D A (1999): The *af* gene regulates timing and direction of major developmental events during leaf morphogenesis in garden pea (*Pisum sativum*). Ann. Bot. 83: 117-128

Vilmorin P D, Bateson W (1911): A case of gametic coupling in *Pisum*. Proc. R. Soc. B 84: 9-11

Warkentin T, Klassen E, Bing D, Lopetinsky K, Kostiuk J, Barlow B, Ife S, Tar'an B, Vandenberg B (2009): CDC Tucker and CDC Leroy forage pea cultivars. Can. J. Plant Sci. 89: 661-663

Yaxley J L, Jablonski W, Reid J B (2001): Leaf and flower development in pea (*Pisum sativum* L.): Mutants *cochleata* and *unifoliata*. Ann. Bot. 88: 225-234

Young J P W (1983): Pea leaf morphogenesis: A simple model. Ann. Bot. 52: 311-316